Dietary variation among indigenous Nicaraguan horticulturalists and their dogs: an ethnoarchaeological application of the Canine Surrogacy Approach

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Abstract

Dietary reconstruction via stable isotope analysis is an important part of the study of past populations, but can raise issues in many parts of the world where human remains are scarce, absent, or restricted due to ethical concerns. Given these issues, some researchers have used domesticated dogs as human dietary proxies via the Canine Surrogacy Approach (CSA). We performed carbon and nitrogen stable isotope analysis on the hair of 304 humans and 57 dogs from 45 households in two contemporary indigenous communities in Nicaragua's Bosawas Biosphere Reserve to explore whether dogs function as dietary proxies for their human owners in this Neotropical horticulturalist context. While CSA is broadly viable at these study sites, on a more precise scale the diets of dogs do not reflect the diets of their owners. This raises questions about the applicability of CSA to archaeological contexts, suggesting that relying on dogs as dietary proxies may overlook key variation in past human diets.

Keywords: canine surrogacy approach; ethnoarchaeology; stable isotope analysis; Nicaragua; dogs; Bayesian inference

1. Introduction

Dietary reconstruction is an important part of the study of past populations and stable isotope analysis has become a widely used tool to interpret past diet. While it is a well-established archaeological method, there are many regions of the world where access to human remains for any destructive analysis is prohibited due to concerns about ancestral and ethical treatment of the dead (Katzenberg 2001, Hublin et al. 2008). The use of dogs as dietary proxies for humans may circumvent the need for human tissue samples, especially in cases of important, scarce, or absent remains. This method is based on the premise that dogs are scavenging or being provisioned by owners with food from the local human diet, therefore exhibiting dietary isotope results that mirror contemporaneous human populations. Dogs are increasingly being used as human dietary proxies in archaeological contexts and recently this methodology was outlined and reviewed by Guiry (2012, 2013), who labeled it the Canine Surrogacy Approach (CSA).

Early uses of CSA include Burleigh and Brothwell (1978), who first used dogs to infer maize consumption in Peru (see also Katzenberg 1988, 1989, Murray and Schoeninger 1988, Edwards et al. 2016) and Noe-Nygaard (1988) who used dogs to reconstruct human diets across the Mesolithic-Neolithic transition in Denmark. Cannon et al. (1999) used CSA to suggest dogs can proxy human diets when no human remains are available. Since then, many others have used archaeological dog remains to help reconstruct human dietary practices (e.g., White et al. 2001, Allitt et al. 2008, Barton et al. 2009, Choy and Richards 2009, Schulting and Richards 2009, Rick et al. 2011, McManus-Fry et al. 2016, Edwards et al. 2016, Edwards et al. 2017). Overall, many reports suggest that dog diets appear to reflect general similarities to those of humans (within 2-3‰ in both $\delta^{15}N$ and $\delta^{13}C$; see Guiry 2012). Yet, others show a disparity in stable isotope values between humans and dogs (Eriksson and Zagorska 2003, Richards et al. 2009, Byers et al. 2011, Pearson et al. 2015, Tsutaya et al. 2014, Ames et al. 2015, Laffoon et al. 2017), which raises doubts about the applicability of CSA in archaeological contexts.

To evaluate how well dog diets reflect human diets, here we apply CSA to all humans and dogs from 45 households in two neighboring rural Nicaraguan villages, providing a complete picture of human-dog dietary breadth across two communities. To our knowledge, this study represents the first broad application of CSA to ethnographic data (see Van der Merwe et al. 2000 and Tankersley and Koster 2009 for previous ethnoarchaeological CSA applications). Testing CSA in communities with known

socioeconomic and subsistence information allows us to contextualize the implications of the isotope results and their interpretations. In this study we employ both a broad species-level (human/dog) application of CSA (e.g., Noe-Nygaard 1988, Cannon et al. 1999, West and France 2015, Edwards et al. 2017) and a household-level application between individual dogs and their human owners (e.g., Tifental 2016). Household-level studies have been less common in the archaeological literature due to the difficulty of linking a particular dog to a specific household. Our method allows for the incorporation of predictor variables, including household wealth and the age and sex of both humans and their dogs. This permits us to determine how well dog diets perform as a human dietary proxy at our sites. We examined dog-human diet association at both the species and household levels, while isolating important variables that may affect this relationship. Our results, combined with detailed ethnographic data, provide a foundation for understanding "living assemblage" human-dog dietary relationships and inform future CSA applications.

2. Study sites

Fieldwork for this study took place in two indigenous communities in Nicaragua's Bosawas Biosphere Reserve, part of the largest tract of unbroken neotropical rain forest north of Amazonia (Figure 1). The communities, Arang Dak and Suma Pipi, are inhabited by indigenous Mayangna and Miskito horticulturalists (Koster et al. 2013). Their primary crops include manioc, bananas and plantains, beans, and rice. Maize is also cultivated but is less common than beans and rice, and compared to other locations in Central America (e.g., Pacheco-Cobos and Winterhalder 2015), maize is less important as a staple crop. The residents of these communities also keep domestic animals, including cows, pigs, and fowl. However, cattle are rarely consumed and kept primarily as a store of wealth that can be sold when there is a need for cash. Much of the dietary protein in this setting is from harvested fish and game (Koster 2007; Koster and Leckie 2014). Although fishing hooks are useful during the rainy season, there are few sediments in the freshwater river during the dry season, which then permits fishermen to use bows and homemade harpoons. Fishing productivity therefore increases greatly from February through April (Koster et al. 2016). Villagers also have access to some processed packaged foods imported from outside the reserve, which may have an effect on their dietary isotopes (Somerville et al. 2017).

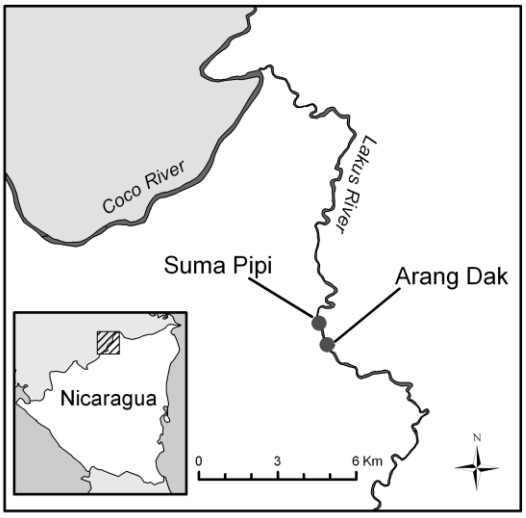

Figure 1. Map of the study communities.

While dogs are a regular part of the Suma Pipi and Arang Dak communities, only two-thirds of households own them. Most dog-owning households have three or fewer (the average is 1.7), but one has four dogs and another household – the wealthiest household in this sample – owns five. Mayangna and Miskito hunters largely rely on their dogs to locate game animals, particularly focusing on terrestrial mammals such as tapirs, agoutis, pacas, nine-banded armadillos, and collared peccaries (Koster 2006; Koster 2008a; Koster 2008b). Dogs vary considerably in their hunting ability, and male dogs seem to exhibit moderately greater performance (Koster and Tankersley 2012). Dogs also improve as they age, and few dogs under three years old are able to chase and corral collared peccaries. Yet, although some dogs help to harvest hundreds of kilograms of meat per year, others provide essentially no benefits as hunting companions and they rarely join their owners on excursions into the forest (Koster and Noss 2014). However, despite widespread ethnographic reports that talented hunting dogs receive favorable treatment and provisioning from their owners (Koster 2009; see Supplemental Figure 1), there is little isotopic evidence that the diets of dogs in this setting vary as a function of their hunting ability (Koster and Tankersley 2012).

Dogs in the study communities are fed by their owners, and it is common to observe women spooning rice or cooked bananas onto the porch for the dogs to consume. It is less common to observe dogs being fed purchased foods or meat. Dogs rarely range alone beyond the boundaries of the community or attempt to provision themselves (Koster and Noss 2014; see also Lupo 2012) and feeding dogs that belong to other households is rare. Despite the provisioning from owners, veterinary examinations of the dogs indicate that most are malnourished, which is exacerbated by high parasitic loads, disease burden, anemia, and dehydration (Fiorello et al. 2017). Although dogs in other settings regularly consume human feces (Tankersley and Koster 2009), the presence of latrines in these communities largely precludes this possibility for the dogs in this study. Overall, the annual mortality rate of the dog population is high, approximately 50%, and leading sources of mortality include attacks by jaguars, snakebites, and unspecified illnesses.

The study communities are characterized by considerable wealth inequality. During the 2013 study period, the household-level Gini coefficient (where 0 represents perfect equality and 1 represents maximal inequality; Gini 1912, Tucker et al. 2015) was 0.60. There is evidence that wealthier households consume healthier diets than those of poorer households, as children in wealthier households exhibit higher height-for-age and weight-for-age measurements (Winking and Koster 2015). Wealthier households are also more likely to purchase locally harvested meats and processed foods that are imported from outside the reserve, such as cookies, crackers, soup mixes, canned sardines, powdered drink mixes, and carbonated soft drinks (Cooper et al. 2018). Despite considerable household-level heterogeneity in wealth and hunting productivity, food sharing between families reduces some of the variation in diets across families (Koster 2011).

3. Factors affecting comparative dimensions of CSA

Guiry (2012) set out a framework for the application of CSA, noting that it is a "theory through which dogs can be viewed as a form of dietary analogy for contemporaneous humans" (2012: 352). CSA applications make two assumptions: firstly, that dogs have access to human food (presumably in roughly the same proportions as humans) and secondly that humans and dogs metabolize and incorporate their food in similar ways to produce similar isotope results. While noting that many CSA applications found general similarities (within 2-3‰ in both $\delta^{13}C$ and $\delta^{15}N$) between human and dog isotope results, Guiry also referenced "disagreement in the literature with regards to what constitutes stable isotope value similarities that are "close enough" for dogs to provide credible information on human dietary activities" (2012: 359). This debate remains unresolved, but Guiry suggested dividing CSA applications into direct (e.g., dog diets transposed onto human diets) and indirect (e.g., dog diets indicating the use of special

foods, like maize) analogies. He also outlined the biological, behavioral, cultural and environmental factors that may influence how dog diets can be used to proxy human diets. Following Wylie (2002: 147), Guiry (2012: 362) noted that "these factors can be neutral (that is they are unlikely to influence dog diet relative to human diet), negative (they are likely to skew dog diet such that it is less isotopically consistent with human diet), or positive (they are likely to contribute to a convergence of dog and human diet)." The benefit of our study as the first broad ethnoarchaeological application of CSA is that we can directly test this CSA framework to a known population, controlling for the variables which may affect a human-dog dietary proxy relationship.

Following Guiry's (2012: 362-368) framework on a point-by-point basis, here we individually outline the potential influencing factors affecting the degree to which dog diets are analogous to human diets at our Nicaraguan sites.

Life Span and Bone Remodeling

Guiry (2012: 363) outlines the potential problems associated with comparisons of human and dog bone experiencing differential remodeling rates. Given that we sampled only human and dog hair for this study, we do not address the issues associated with bone growth and remodeling which may affect stable isotope composition from bone collagen studies.

Domestic, Wild, or Hybrid

Guiry (2012: 363) raises potential issues associated with the archaeological sampling of canids which may not be domesticated dogs or representing hybrid individuals. The only other canids in Nicaragua are the gray fox (*Urocyon cinereoargenteus*) and the coyote (*Canis latrans*). Coyotes have only been present in Nicaragua since the 16th century (Hidalgo-Mihart et al. 2004) and are uncommon, especially in the denser tropical forest regions. There have been no reported coyotes or gray foxes at or near our sites and there is no reported hybridization between either foxes or coyotes and dogs in Nicaragua. All of our samples come from non-hybridized domesticated dogs.

Caecotrophy Among Dogs

Guiry (2012: 364) makes an important comment on the extent to which caecotrophy, the consumption of feces, in dogs may affect their $\delta^{15}N$ values, noting it is unclear whether the values would increase or decrease. The Miskito and Mayangna villages have latrines, so dogs have little access to human feces. In contrast, domestic livestock in the villages include cattle, pigs, and fowl (chickens, ducks, and turkeys), and these animals freely defecate in and around the villages and dogs have the opportunity to consume the feces. Dogs also sometimes eat the feces of wild animals while on hunting trips. Cattle freely graze within the village and surrounding "pasture," while pigs, the ownership of which is widespread, are provisioned with maize and manioc.

Dog Worship

Guiry (2022: 364-365) notes that some dogs may be fed restricted diets due to spiritual or ritual reasons, leading to dietary signatures unlike those of humans from the site. In contrast to some archaeological evidence for ritual uses of dogs in the Neotropics that could lead to significant isotopic variation (White et al. 2001, White 2004, White et al. 2006), Miskito and Mayangna dogs are not part of any ritual context that results in some dogs being provisioned differently.

Dog Consumption

Guiry (2012: 365) observes that the consumption of dogs by humans would result in slightly elevated human $\delta^{15}N$ values, given similar diets in both humans and dogs, due to the trophic level effect. Villagers at our sites do not consume dogs, so this does not affect our analysis.

Separate Treatment of Differing Dog Breeds

Guiry (2012: 365-366) hypothesizes that dogs bred for different roles within a group (e.g., for hunting or consumption) may have differential diets related to those roles, which were not analogous to human diets. At Arang Dak and Suma Pipi, dogs are rarely a true breed (Koster 2007). Like other village dogs in the Neotropics, they are mostly short-haired, small to medium-sized mutts (Oberg 1949, Wagley 1977, Lauer 2005, Kohn 2007) and not intentionally bred for any particular role.

Technological Change

Similar to dogs used for ritual purposes or breeds that fill specialized roles, Guiry (2012: 366) notes that some dogs representing technological changes (e.g., for traction or guarding, cf. Serpell 1995) may also be fed specific diets which do not reflect the diets of their human keepers. Aside from hunting (discussed below), dogs in these communities are not used as technology, though they do provide some measure of protection for homes against burglary (Koster 2007:129).

Economic Transactions

Guiry (2012: 366) and others (Gosden and Pavlides 1994, Eriksson and Zagorska 2003) have raised issues with the use of isolated dog elements, like teeth, in CSA applications. These elements may be traded between groups with different dietary regimes, thus they may not reflect the diet of the local community and should be analyzed with caution. Dog elements are not used or traded in any way in the villages we studied, so should have no reason to end up anywhere outside the villages.

Dependence on Dog Services

Guiry (2012:367) suggests reliance on dogs for services, such as transport, may lead to human provisioning and a potentially positive CSA application, especially in the northern latitudes. Contrary to this, some ethnographic sources suggest northern pack dogs are provisioned with a diet different from that of humans (Macpherson and Manning 1961, Zagoskin 1967, Savelle 1984, Andersen 1992), often with a substantial reliance on fish, which is seen as a high-quality, low-cost food, being easily caught and dried or frozen. A similar marine-based dog diet, in contrast to a more varied human faunal assemblage, has been documented at coastal archaeological sites (e.g., Ames et al. 2015).

The importance of a dog in hunting or other economic activities is not necessarily tied to a different or improved diet. While some hunting dogs are provisioned with special items like a pregnant prey's fetus (Sponsel 1981, Forline 1997) or internal organs (Montiel Ortega et al. 1999) of captured prey animals, there are many examples of hunting dogs being underfed. Some ethnographers report hunting dogs that survive by scavenging food scraps, refuse, or human excrement (Bergman 1980, Dumont and Hurlich 1981, Werner 1984).

At Arang Dak and Suma Pipi, not all dogs are considered hunting dogs, and some dogs exist only as pets or "house dogs". Although there is a high level of agreement among villagers about which hunting dogs are good, and these dogs generally appear to receive better care (Koster 2007), Koster and Tankersley (2012) previously found no correlation between an improved diet and hunting dog ability at the sites. While some researchers note hunting dogs may be purposely kept hungry to improve hunting motivation and effectiveness (Metzger and Morey 1983, Crocker 1990, Holt et al. 2004), Miskito and Mayangna hunters do not appear to subscribe to this philosophy and may give their hunting dogs small amounts of meat when an animal is killed or cooked (Koster 2007, Koster and Tankersley 2012).

There is often an assumption that dog burials are a more reliable proxy for human diets, as these dogs were revered in some way by humans (e.g., Hogue 2002). Conversely, previous stable isotope analysis of dog burials at Arang Dak and Suma Pipi found broad ranges in both $\delta^{13}C$ and $\delta^{15}N$ values, with some $\delta^{13}C$ values that reflect maize consumption (-11.6‰) and others that do not (-22.2‰) (Tankersley and Koster 2009). Also, active hunting dogs are more likely to die during hunts and are buried in the forest, while other dogs are more commonly buried in the village, raising the question of bias in the archaeological sampling of village-buried dogs.

Isolation

Guiry (2012: 367) documented a problem among some groups in trading dogs to nearby neighbors, only to have the loyal dogs return (Mandelbaum 1979:66). As a result some groups traded dogs only with distant neighbors or passing travelers. Some researchers have documented significant movement and exchange of dogs in various cultural contexts (Howard 2001, Mans 2012, Laffoon et al. 2017), raising potential issues in the dietary relationship between humans and their non-native dogs.

There is a long history of dogs being purchased or traded in the ethnographic literature of the Neotropics (Schomburgk 1922, Descola 1996, Koshear 1995, Howard 2001), including near the Bosawas Reserve (Belt 1911). Many Neotropics village dogs have been imported from nearby cities (Fiorello et al. 2006, Kohn 2007), potentially leading to significant differences in dietary intake. The Miskito and Mayangna in our study live in a fairly isolated location and dogs are usually acquired as puppies, whether purchased, received as gifts, or kept from a litter. Only dogs beyond weaning age were used in our study. Sometimes older dogs are sold, particularly those with a good reputation for hunting, but most sales are to other members of the community (Koster 2007). However, if local dogs were traded to outside locations, such as villages of intensive agriculturalists, and then died shortly after arrival, they would reflect the more terrestrial diet of Arang Dak and Suma Pipi as opposed to the maize-based diet of their new owners. Archaeologically, in regions where dogs may have been traded between hunting and farming communities, or to passing travelers, this variation would prove problematic for CSA applications. This may be addressed by utilizing stable isotopes that reflect mobility, such as strontium (Bentley 2006, Laffoon et al. 2017), but raises important questions about the natal origins of dogs being used in these applications.

4. Materials and methods

In February and March of 2013, hair samples were obtained from all residents and dogs who were present in the communities during data collection of anthropometric measurements on the human residents. Although we sampled infants and suckling puppies, we exclude them from this study due to the trophic effects of breastfeeding and weaning (Tsutaya and Yoneda 2015). For long-haired humans, we attempted to collect samples of hair that were close to the scalp. All dogs at these field sites have short hair, and samples were obtained from the base of the tail. In total, we analyzed 304 humans and 57 dogs between both communities.

A census from the same field season provides demographic information, particularly age and sex, on the humans and the dogs and the wealth of their respective households (n = 45). Wealth is calculated as the cumulative value of key household possessions, such as livestock, firearms, portable radios, and flashlights (Winking and Koster 2015).

Hair has been shown to record dietary information in the form of stable carbon and nitrogen isotope ratios (DeNiro and Epstein 1978, 1981), including significant differences in dietary regimes between individuals (O'Connell and Hedges 1999, Petzke et al. 2005, Somerville et al. 2017). Due to its fast rate of growth, stable chemistry after formation, and ability to be sampled non-invasively from living individuals, it makes an ideal material for studying living populations (LeBeau et al. 2011, White et al.

2011). While human hair grows at a rate of about 1 cm per month (Valković 1977), research on dog hair growth seems to vary based on the individual, breed, body location of the hair, and season of the year, though it also averages around 1 cm per month (Al-Bagdadi 1977, Gunaratnam and Wilkinson 1983, Diaz et al. 2004). Previous comparative studies of human and dog hair stable isotopes have assumed a 1 cm per month growth rate for both (Bol and Pflieger 2002). The dogs at our site are mostly short-haired mutts. Hairs were collected in February and March, which falls in the hot, dry season. There is some evidence that short-haired dog hair in the tropics grows less and sheds more in the hot season (Favarato and Conceição 2007), but similar seasonal shedding has been observed in humans (Williams et al. 2011). Given this, we assume similar rates of seasonal hair growth and shedding in humans and dogs at the sites.

Carbon isotope analysis of hair keratin compares the ratio of ^{13}C /^{12}C (expressed as $\delta^{13}C$) resulting primarily from differential consumption of C_3 and C_4 plants. C_3 plants have lower $\delta^{13}C$ values (averaging -27.0‰; Kohn 2010; O'Leary 1988; Smith and Epstein 1971) and include bananas and plantains, manioc, beans, and rice as part of traditional Miskito and Mayangna diets. C_4 plants have higher $\delta^{13}C$ values (averaging -12.5‰; O'Leary 1988; Smith and Epstein 1971) and include maize and some imported packaged foods at our sites. The $\delta^{13}C$ values in hair keratin are approximately 4‰–5‰ higher than dietary $\delta^{13}C$ values (Hedges, Rush, and Aalbersberg 2009, Yoshinaga et al. 1996).

Nitrogen isotope analysis of hair keratin compares the ratio of $^{15}N/^{14}N$ (expressed as $\delta^{15}N$), used to determine the individual's trophic level based on a ~3‰–5‰ ^{15}N enrichment in tissues at each increasing position on the food chain (Minagawa and Wada 1984, Schoeninger and DeNiro 1984, Lee-Thorp 2008). Because of this relationship, higher $\delta^{15}N$ values are associated with carnivory and the frequent consumption of foods coming from increased $\delta^{15}N$ marine systems (Schoeninger et al. 1983). The offset between dietary protein and hair keratin $\delta^{15}N$ is about 4‰–5‰ (Hedges, Rush, and Aalbersberg 2009; Yoshinaga et al. 1996).

Human hair samples were prepared for isotope analysis and measured at the Department of Anthropology, University of British Columbia (Vancouver, Canada). Dog hair samples were prepared for isotope analysis and measured at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany), following the same protocols. All hair samples were weighed, individually labeled, and prepared for analysis using standard protocols to degrease and clean samples (O'Connell and Hedges 1999, O'Connell et al. 2001, Hedges et al. 2005). Samples were rinsed twice in deionized water to remove debris, sonicated for 10 minutes during each rinse, then soaked in a 2:1 methanol/chloroform solution (30 min; 3x). Following these soaks, the samples were rinsed four times with deionized water, then dried overnight at 30ºC. Once dried, each sample was cut into 1cm-long segments, randomized and packaged into tin weigh boats for analysis.

Carbon and nitrogen isotope analyses were carried out using a MicroCube elemental analyzer coupled to an Isoprime isotope ration-mass spectrometer (EA-IRMS). All isotope data were calibrated using USGS 40 ($\delta^{13}C$ = -26.39, $\delta^{15}N$ = -4.52) and USGS 41 ($\delta^{13}C$ = 37.63, $\delta^{15}N$ = 47.57). Data was scaled to Vienna Pee Dee Belemnite (V-PDB) for carbon and the ambient inhalable reservoir (AIR) for nitrogen. Internal and international standards were used, including USGS 42 ($\delta^{13}C$ = -21.09, $\delta^{15}N$ = 8.05), USGS 43, ($\delta^{13}C$ = -21.28, $\delta^{15}N$ = 8.44), Methionine (internal accepted $\delta^{13}C$ = -28.57, $\delta^{15}N$ = -5.01), and SUBC 1 (internal collagen standard with accepted $\delta^{13}C$ = -13.73, $\delta^{15}N$ = 17.39). Measurement error on the $\delta^{13}C$ and $\delta^{15}N$ values was calculated from the repeat measurements of internal and international standards and was ± 0.2% (1σ) or better.

5. Analysis

Following Guiry's (2012) outline of the Canine Surrogacy Approach (CSA), we begin by making two related predictions about the isotope values of dogs relative to humans. First, we examine across-species differences at the level of the community:

> **Prediction 1:** There are differences in the average isotope values of human samples and dogs' samples at this site.

A lack of statistical support for this prediction would be consistent with the CSA.

We also advance a household-level CSA:

> **Prediction 2:** At the level of the household, there are positive correlations between the values of the human residents and the dogs they own.

In addition to broad predictions about the similarities between the isotope signatures of dogs and human, we also draw on research that shows how dietary variation reflects heterogeneity in wealth (Somerville et al. 2013, Stantis et al. 2015, Waterman et al. 2016). That research leads us to advance an additional prediction about household-level heterogeneity:

> **Prediction 3:** For both humans and dogs, isotope values reflect variation in households' wealth.

Finally, although we had no *a priori* hypotheses about the interaction effects of household wealth and individuals' ages, our exploratory plots of the data suggested that the effect of wealth on human nitrogen values seems to be moderated by the individuals' age. This exploratory analysis therefore leads us to advance the following prediction about isotope variation among humans:

> **Prediction 4:** Older, wealthier individuals have higher nitrogen values than others.

Given our interest in household-level isotopic variation, we employ a multilevel modeling approach for reasons described by McElreath (2015). Whereas anthropologists have recently used multilevel modeling to account for repeated isotope measurements of the same individuals (Fahy et al. 2014) or repeated measurements of the same species (Oelze et al. 2014), this analysis extends the approach to household-level clustering. Furthermore, an evidently novel aspect of our modeling approach is that we model the $\delta^{13}C$ and $\delta^{15}N$ values as the dependent variables in a Gaussian bivariate response model, allowing for correlated random effects across the two functions. In addition, we include binary fixed effects to distinguish the dogs from the humans in the sample, and we allow both the intercepts and these fixed effects for dogs to vary by household (random intercepts and random coefficients, respectively). Assuming Gaussian distributions of the response variables, our base models can be formally notated as follows:

$$\delta^{13}\mathrm{C}_{ijk} = \beta_{0ijk} + \beta_2(\mathrm{dog}_{ijk}) + u_{0jk} + u_{2jk}(\mathrm{dog}_{ijk}) + e_{0ijk}$$

$$\delta^{15}\mathrm{N}_{ijk} = \beta_{1ijk} + \beta_3(\mathrm{dog}_{ijk}) + u_{1jk} + u_{3jk}(\mathrm{dog}_{ijk}) + e_{1ijk}$$

$$\begin{bmatrix} u_{0k} \\ u_{1k} \\ u_{2k} \\ u_{3k} \end{bmatrix} \sim \mathrm{N}(0, \Omega_u) : \Omega_u = \begin{bmatrix} \sigma^2_{u0} & & & \\ \sigma_{u01} & \sigma^2_{u1} & & \\ \sigma_{u02} & \sigma_{u12} & \sigma^2_{u2} & \\ \sigma_{u03} & \sigma_{u13} & \sigma_{u23} & \sigma^2_{u3} \end{bmatrix}$$

$$\begin{bmatrix} e_{0ijk} \\ e_{1ijk} \end{bmatrix} \sim \mathrm{N}(0, \Omega_e) : \Omega_e = \begin{bmatrix} \sigma^2_{e0} & \\ \sigma_{e01} & \sigma^2_{e1} \end{bmatrix}$$

where we model the isotope values of the individuals and dogs in the sample. In this notation, k represents an index for either of the two responses, δ^{13}C or δ^{15}N, i is an index for individual i ($i = 1, \ldots, N$) in household j ($j = 1, \ldots, N$). Each equation has an intercept term (β_{0ijk} and β_{1ijk}), a binary fixed effect variable to distinguish dogs from humans in the sample (β_2 and β_3), a random intercept to account for individuals from different household (u_{0jk} and u_{1jk}), a random coefficient that allows the response to vary for dogs from different households (u_{3jk} and u_{4jk}), and a residual error term (e_{0ijk} and e_{1ijk}). The household-level random effects are assumed to be multivariate normally distributed with zero means and a homogenous 4 × 4 variance-covariance matrix. Similarly, the residual variances are assumed to be normally distributed around means of zero and homogenous 2 × 2 variance-covariance matrix.[1]

The base model presented above does not include fixed effect covariates beyond the intercept terms or the binary variable that distinguishes dogs, but the model can readily be extended to include additional predictor variables, whether defined at the level of the household or the individual. The inclusion of additional parameters alters the predicted values for individuals in the sample and therefore the estimated random effects and their correlations are impacted as well.

The covariates in our models are *sex*, *age*, and *wealth*. See Table 1 for descriptive statistics on individual-level variables. The former is a straightforward binary variable, coded as 1 for males. In order to put the ages of people and dogs on similar scales, the original values for each individual were divided by a value that represents the age of an elderly individual of that respective species, namely 80 for humans and 10 for dogs. After this standardization, for example, an 8-year-old human would have a value of 0.1 whereas an 8-year-old dog would have a value of 0.8.[2] Because of the weaning effect (Schurr 1998), we limit our analysis to humans who are at least 4 years old, the age at which greater than 95% of the children in this setting have reportedly been weaned. We include dogs of all ages while noting that puppies seldom suckle past two months of age.

[1] Note that our model assumes homoscedastic variance across humans and dogs. We used Levene's test to test for unequal variances across species for both the δ^{13}C and δ^{15}N values, and the respective tests did not reveal unequal variances.

[2] The distributions of ages are positively skewed for both humans and dogs, reflecting the high proportion of juveniles and young adults in each population. As a robustness check, we estimated models in which we square-root transformed the variable for age. These models resulted in similar inferences as the ones we present.

Variable	Humans (n = 304)	Dogs (n = 57)
$\delta^{13}C$	−22.5 (0.8)	−22.4 (0.9)
$\delta^{15}N$	9.5 (0.6)	9.5 (0.5)
Age (standardized)	0.2615 (0.19)	0.2269 (0.18)
Male	0.50	0.37

Table 1. Descriptive statistics for the individual-level response variables and covariates, organized by species. We present sample means or proportions with standard deviations in parentheses.

To account for the positive skew that characterizes household wealth, we log-transform this variable. Following this transformation, the variable ranges from 3.04 to 5.72 with a mean of 4.49 and a standard deviation of 0.5.

In addition to our base model, we specify three additional models, one that includes demographic variables as control variables and two further models that test the aforementioned predictions. In all of these models, we specify interaction terms that allow the main effects to be moderated by the binary variable for species. Our final model, which tests our fourth prediction, includes a three-way interaction of the covariates for *species*, *age*, and *wealth* along with the corresponding two-way interaction terms. To compare models, we report the Watanabe-Akaike Information Criterion (WAIC), with lower values indicating preferred models that effectively balance over-parameterization against model fit.

To conduct probabilistic inference of our models' parameters (see Otárola-Castillo and Torquato 2018 for similar archaeological applications) we use Markov chain Monte Carlo (MCMC) methods, as implemented in the BRMS package (Bürkner 2017). We used the package's suggested weakly informative priors for all parameters, reflecting our partial knowledge about their distributions and to ensure a sensible posterior distribution (Gelman 2013: 55). After a burn-in of 1,000 iterations, we sample an additional 20,000 iterations as the basis for inference. Conventional MCMC diagnostics yielded no concerns about the mixing of the MCMC chains.

To calculate the extent to which dogs and humans from the same household exhibit comparably high or low $\delta^{13}C$ and $\delta^{15}N$ values, we computed Pearson's r, the correlation between the predicted values of humans and dogs from the same household. We report the average of the resulting distribution of correlations and the 90% range as credible intervals (see https://doi.org/10.17605/OSF.IO/DBXE9).

6. Results

All samples met with quality control criteria (DeNiro 1985; O'Connell and Hedges 1999; van Klinken 1999). Figure 2 shows the plotted isotope results for both humans and dogs (see Supplemental Figure 2 for household-level plots). Human $\delta^{15}N$ values range from 6.9‰ to 12.8‰ and dog $\delta^{15}N$ values range from 8.4‰ to 10.8‰. Human $\delta^{13}C$ values range from -24.7‰ to -19.0‰ and dog $\delta^{13}C$ values range from -24.3‰ to -20.1‰. See Supplemental Table 1 for raw data.

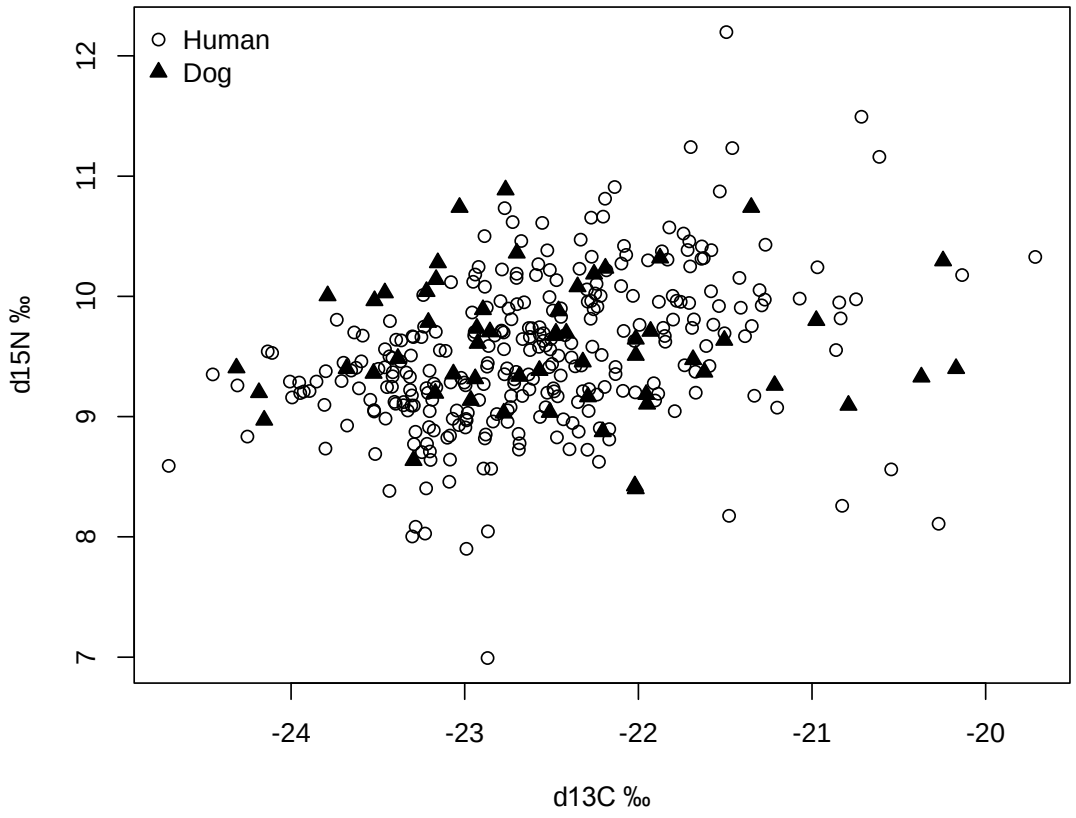

Figure 2. Carbon and nitrogen values for humans and dogs at Arang Dak and Suma Pipi.

The parameters for our models are reported in Table 2. A comparison of the WAIC values indicates that the inclusion of the demographic control variables in Model 1 considerably improves model fit. Whereas the addition of *wealth* and the corresponding interaction terms evidently does not improve model fit, the three-way-interaction terms in Model 3 results in the most preferable model.

Coefficients	**Base model**		**Model 1**		**Model 2**		**Model 3**	
Variable	*Carbon*	*Nitrogen*	*Carbon*	*Nitrogen*	*Carbon*	*Nitrogen*	*Carbon*	*Nitrogen*
Intercept (Human Ref)	-22.57 (0.09)	9.52 (0.06)	-23.04 (0.10)	9.14 (0.08)	-24.90 (0.69)	8.20 (0.42)	-25.22 (0.85)	8.43 (0.63)
Dog	0.08 (0.15)	0.06 (0.10)	0.14 (0.22)	0.31 (0.15)	0.10 (0.22)	0.29 (0.15)	0.02 (2.01)	2.04 (1.33)
Age			1.81 (0.18)	1.44 (0.15)	1.81 (0.18)	1.44 (0.15)	1.32 (1.90)	-2.10 (1.57)
Dog * Age			-0.24 (0.57)	-0.81 (0.45)	-0.33 (0.57)	-0.88 (0.45)	15.16 (6.42)	-3.50 (4.60)
Male			-0.06 (0.07)	-0.02 (0.06)	-0.06 (0.07)	-0.02 (0.06)	-0.06 (0.07)	-0.03 (0.06)
Dog * Male			0.27 (0.20)	0.03 (0.16)	0.25 (0.20)	0.02 (0.16)	0.24 (0.20)	0.07 (0.16)
Log (Wealth)					0.39 (0.15)	0.21 (0.09)	0.49 (0.19)	0.16 (0.14)
Dog * Wealth					-0.68 (0.32)	-0.31 (0.20)	-0.02 (0.43)	-0.37 (0.28)
Age * Wealth							0.11 (0.41)	0.78 (0.34)
Dog * Age * Wealth							-3.14 (1.31)	0.48 (0.94)
Human-dog Correlations								
Carbon	0.30 (0.01, 0.60)		0.18 (-0.07, 0.44)		0.31 (0.02, 0.60)		0.30 (0.02, 0.58)	
Nitrogen	0.40 (-0.11, 0.97)		0.18 (-0.34, 0.74)		0.16 (-0.40, 0.79)		0.11 (-0.42, 0.75)	
Variances								
Random Intercept	0.26 (0.07)	0.12 (0.05)	0.25 (0.07)	0.12 (0.05)	0.19 (0.07)	0.09 (0.16)	0.19 (0.07)	0.08 (0.05)
Species Coefficient	0.44 (0.15)	0.12 (0.12)	0.61 (0.16)	0.17 (0.12)	0.64 (0.16)	0.17 (0.12)	0.59 (0.18)	0.15 (0.13)
Residual	0.42 (0.03)	0.29 (0.02)	0.31 (0.02)	0.22 (0.02)	0.31 (0.02)	0.22 (0.02)	0.30 (0.02)	0.22 (0.02)
WAIC	1341.7 (58.4)		1201.6 (58.8)		1205.5 (59.2)		1192.4 (60.1)	

Table 2. Model output. Reported quantities are the means (standard deviations in parentheses) from the posterior samples of the MCMC chains. Asterisks between terms denote interaction effects. For the

human-dog correlations, the reported values are the means calculated from the posterior samples and the quantities in parentheses are the 90% credible intervals of those calculations.

Prediction 1: Species-level differences

Our base model permits a test of Prediction 1, and the model's parameters for dogs' $\delta^{13}C$ ($\beta = 0.09$) and $\delta^{15}N$ ($\beta = 0.07$) show that, on average, the isotope values are expected to be largely identical for humans and dogs. At the level of the community, in other words, these results provide support for the CSA.

Prediction 2: Household-level correlations

Do humans and dogs from the same household exhibit similar isotope signatures? Contrary to our predictions, strong correlations are not evident in the statistical models. In general, the correlations are positive ($\delta^{13}C = 0.30$ and $\delta^{15}N = 0.40$ in the base model), but correlations are modest and the credible intervals are wide. The correlation for nitrogen particularly weakens once the effects of covariates are included in the models. Together, these results suggest that dogs are imperfect proxies for dietary inferences about the humans with whom they reside.

Prediction 3: Wealth as a predictor of isotope variation

In Model 2, we add *wealth* as a predictor variable, which exhibits a positive effect on both $\delta^{13}C$ ($\beta = 0.39$) and $\delta^{15}N$ ($\beta = 0.21$) in human diets. Consistent with our third prediction, that is, humans in wealthier households consume more foods that increase their $\delta^{13}C$ and $\delta^{15}N$ values, respectively. Notably, the effects are attenuated for dogs, particularly for $\delta^{13}C$ ($\beta = -0.68$). This result suggests that the effects of wealth do not entail the same benefits for dogs as they do for their owners (Figure 3).

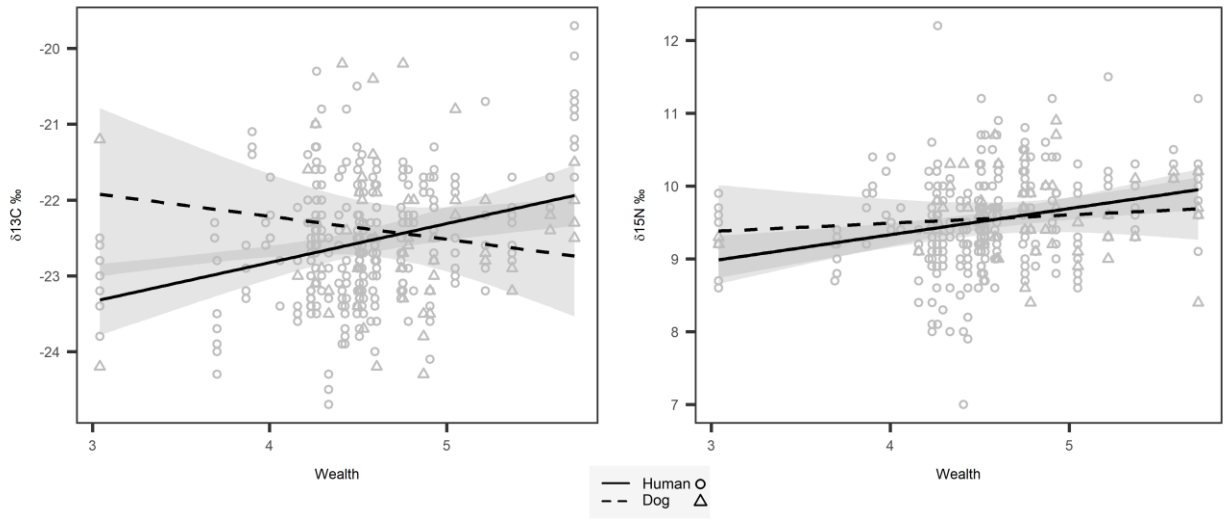

Figure 3. Isotope values as a function of wealth. Circles denote humans, and triangles denote dogs. Gray shading reflects 95% intervals of simulated predictions from the posterior samples. Model predictions assume female individuals of ages at 25% of maximum lifespan for the respective species.

Prediction 4: Interactions of age and household wealth

Model 3 reveals diverse effects of the interaction of *age* and *wealth* for humans and dogs, which we display in Figure 4. For human δ^{13}C, the main effect of wealth ($\beta = 0.49$) continues to suggest that wealthier households consume more foods that increase δ^{13}C values, and the weak interaction term ($\beta = 0.11$) suggests that this effect is not moderated by age. For δ^{15}N, by contrast, the informative interaction term ($\beta = 0.78$) suggests that the benefits of wealth are largely consolidated among the older individuals from wealthier households.

The δ^{13}C of dogs reveal a divergent pattern, as dogs from poorer households are predicted to have a higher δ^{13}C value as they age than their counterparts in wealthier households ($\beta = -3.14$). The δ^{15}N of dogs from wealthy households, by contrast, tend to mirror the increase seen among wealthier humans, but there is little overall evidence to conclude that *wealth* moderates the dogs' δ^{15}N isotope values across the lifespan ($\beta = 0.48$).

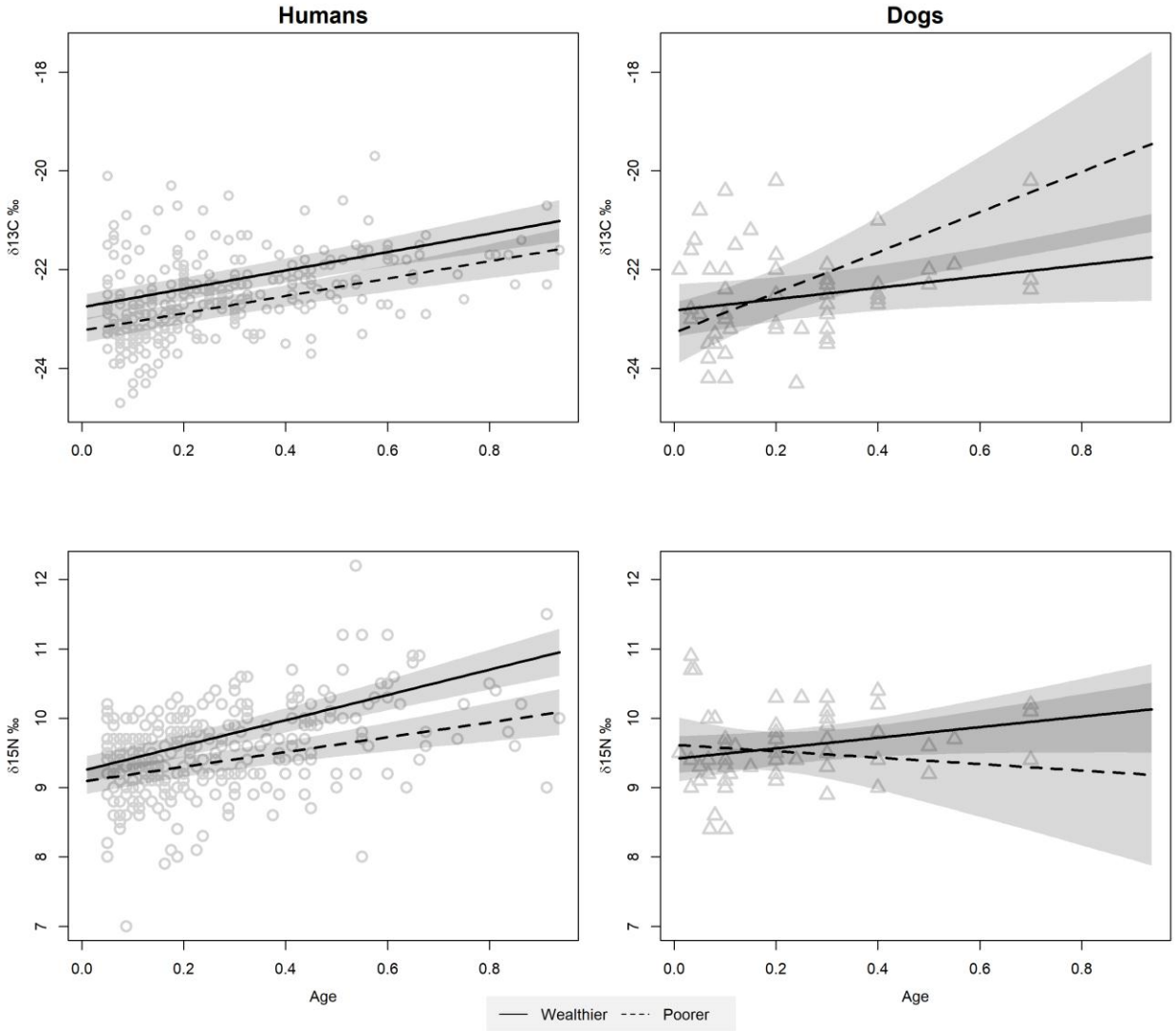

Figure 4. Isotope values as a function of age, moderated by household wealth. Gray shading reflects 95% intervals of simulated predictions from the posterior samples. Predictions are calculated for households

with respective wealth values of 3.05 and 5.6 on the logarithmic scale. Model predictions further assume female individuals.

7. Discussion

Because the overall values for humans and dogs are broadly comparable, our results suggest that the Canine Surrogacy Approach (CSA) functions at our sites on a community level. There are evident limitations to CSA applications, though, as the human-dog correlations do not hold at the household level, suggesting that dog diets do not necessarily reflect the diets of their owners. These results therefore suggest that CSA may be suitable for community-level dietary averages, but there are limitations to dogs' usefulness as straightforward isotope proxies for the human residents of their households.

Predictors of isotopic variation

At these sites, $\delta^{13}C$ and $\delta^{15}N$ vary as a function of wealth, as wealthier households exhibit greater consumption of C_4 and animal products than poorer households (Figure 2). This result therefore echoes a large body of archaeological research showing that wealthier households parlay their wealth into high-status, nutritious diets (e.g., Somerville et al. 2013, Stantis et al. 2015, Waterman et al. 2016). Because wealthy households keep more domestic animals and purchase more harvested meat, their higher $\delta^{15}N$ values are unsurprising. Given the relative unimportance of maize as a staple crop, however, the source of the association between wealth and $\delta^{13}C$ is less clear. One possibility is that pigs and fowl are routinely provisioned with maize, resulting in $\delta^{13}C$ values in the meat that is disproportionately consumed by wealthy households. Another possibility is that wealthier households consume more processed foods, which may contain corn oil and corn syrups derived from C_4 plants corresponding to higher $\delta^{13}C$ values (Jahren et al. 2006).[3] Although the primary source of the $\delta^{13}C$ is not clear, it is evident that dogs in wealthy households do not partake in the consumption of these foods. To a lesser extent, this generalization may be true for $\delta^{15}N$ values as well. However, $\delta^{13}C$ enrichment in some dogs, especially older, poorer dogs, may be related to scavenging livestock feces, particularly that of pigs provisioned with maize. Local residents also report that hungry dogs are more likely to consume the feces of calves that are not yet weaned, and thus on a rich milk-based diet. In archaeological contexts where dogs had access to livestock or wild animal feces, their isotope values may partly reflect the consumption of these feces.

Our control model (Model 1) revealed the main effects of *age*, suggesting that older humans exhibit higher $\delta^{13}C$ and $\delta^{15}N$ values. As noted, our exploratory plots of the data led us to identify an evident interaction between *age* and *wealth*, as in Model 3. When predicting $\delta^{13}C$, however, the interaction term was uninformative. That is, although these two variables independently exhibit positive effects on human $\delta^{13}C$ in Model 2, there is little statistical support for a moderating effect in Model 3. When predicting human $\delta^{15}N$, by contrast, Model 3 reveals an interaction between *wealth* and *age*, as the predicted values are highest for elderly individuals from wealthy households. We emphasize again that we had no *a priori* hypotheses about these effects, but we draw on our ethnographic insight to offer a possible explanation for the age-related effects. That is, our research on food sharing in this setting has revealed the importance of meat sharing among parents and offspring (Koster 2011). When a successful hunter returns with harvested game, for instance, he almost invariably delivers a portion to his parents. Although it is not immediately clear how this normative altruism toward elders could result in elevated

[3] Notably, the household that exhibits the highest $\delta^{13}C$ value is one that maintains a small store from which they sell processed foods that have been imported into the reserve. Members of this household can routinely be observed consuming these products in between meals.

$\delta^{15}N$ among older individuals in wealthier households, we tentatively speculate that elders in such households may feel less onus to share meat with other family members.

For dogs, Model 3 reveals contrasting effects, namely that older dogs from poorer households have the highest predicted $\delta^{13}C$ values. However, there is evidently little interaction between *age* and *wealth* for dogs' $\delta^{15}N$ values. Previously, researchers have noted consistently lower $\delta^{15}N$ values in dog diets as compared to local humans at archaeological sites (Cannon et al. 1999, Hogue 2003, Kusaka et al. 2008, Katzenberg 2006, Katzenberg et al. 2010). Several observations have been made in an attempt to explain this difference, including trophic level shifts as a result of human consumption of dog meat (Richards et al. 2009), coprophagy by dogs (Cannon et al. 2009, Allitt et al. 2008), and differences in human and dog metabolisms and tissue isotope incorporation (Clutton-Brock and Noe-Nygaard 1990, Jay and Richards 2006). At our sites, average $\delta^{15}N$ values between humans and dogs show little difference. Humans also do not consume dogs, nor do dogs consume human feces. We can offer few comments on metabolic variation among dogs and humans in this study, but we highlight the age-related variation and interactions with wealth in case future research addresses analogous effects in other settings. For similar reasons, we note that *sex* evidently has minimal effects on dietary variation, whether for the humans or the dogs in this sample, though sex-based dietary variation may be relevant for CSA applications at other sites (Cheung et al. 2017, Dong et al. 2017).

Additions to the Guiry CSA Framework

In addition to the factors already documented in Guiry's (2012) framework, we include here a number of additional factors, including sampling strategies, that potentially affect applications of the Canine Surrogacy Approach, particularly in archaeological contexts.

Special foods

In Arang Dak the average household consumes maize approximately 22 days a year (Koster 2007). C_4 plant foods like maize are typically associated with $\delta^{13}C$ values greater than -19‰ (O'Leary 1988, Schwartz and Schoeninger 1991, Schoeninger and Moore 1992, Schurr 1992), yet Tankersley and Koster (2009) previously noted that neither human or dog hair samples in a test household with known maize consumption produced values greater than -19‰. Furthermore, only 6% of dog hair samples from across the entire village produced a signature of maize consumption. Tankersley and Koster (2009) suggest significantly greater amounts of maize need be consumed to produce $\delta^{13}C$ values greater than -19‰. While CSA may detect maize and other C_4 plant consumption in significant quantities (e.g., Barton et al. 2009), there seems to be an increased possibility for false negatives given low-level consumption.

Additionally, there may be differential consumption by dogs of certain food products, including maize, if these products are seen as limited, high or low status, or forbidden. For example, dogs may be fed food items not consumed by humans, such as the meat of tabooed species (Sponsel 1981:192, Descola 1996:233). Koster (2007) previously noted that all the villagers at Arang Dak and Suma Pipi consider certain animals, such as giant anteaters, sloths, tayras, and all species of rats, bats, and skunks, to be inedible. Other animals, such as howler monkeys, coatis, and pumas, are variably consumed across individuals and households. Tabooed species are sometimes accidentally killed by hunters, mauled and killed by dogs, or killed by hunters to protect dogs. If one of these animals is killed during a hunt, dogs are occasionally able to consume it, further complicating a proposed analogous relationship between human and dog diets at our sites.

The regular consumption of bone by scavenging dogs may also affect the level at which dogs can be used as human dietary proxies. For example, higher carbon values in older, poorer dogs at our sites may be the result of several factors, including the more frequent consumption of bone, which is up to 2.5 (fish) to 4% (mammal) higher in $\delta^{13}C$ than muscle (Schoeninger and Deniro 1984, Misarti et al. 2009).

Future ethnoarchaeological applications of CSA should focus on whether bone consumption in dogs varies by age and household wealth and whether bone-scavenging dogs have increased carbon values as compared to dogs that do not scavenge bones at the same site.

Types of sample

No human or dog at Arang Dak or Suma Pipi had $\delta^{13}C$ values greater than -19‰, despite direct maize consumption, the consumption of maize-provisioned livestock, and the consumption of processed foods with corn-based products. Even in a previous bone collagen analysis from the sites (Tankersley and Koster 2009), only 5 of 12 dogs analyzed showed evidence of maize in their diet. Given this, we would suggest that the use of hair for stable isotope analysis does not appear to be a good indicator for the identification of low-level maize consumption. Bone collagen appears to give moderately better, but still weak results.

Sample size

The archaeological record represents only a limited portion of a living population. Sampling further reduces the total population analyzed and CSA applications have routinely used fairly low dog samples sizes (Guiry 2012). Small sample sizes of dog bones used for CSA may inadvertently lead to sampling only dogs at extreme ends of dietary variation or dogs with specialized diets. For example, the sampling of village-buried dogs may reflect the diets of pet dogs instead of hunting dogs, which often die and are buried in the forest. At our sites, a small sample size may inadvertently capture the diet of dogs from only one household, overlooking the actual range of household-level dietary variation among both dogs and humans. In previous isotope analyses from our sites (Tankersley and Koster 2009), inter-individual variation in 34 dog hair samples was up to 5.9‰ for $\delta^{13}C$ and 2.9‰ for $\delta^{15}N$. For the 57 dog hair samples from this study, the range of variation in $\delta^{13}C$ is 4.5‰ and 2.6‰ for $\delta^{15}N$. These values represent a wide range of dietary variation within the dogs alone and similar ranges of variation may not be captured given smaller sample sizes, such as those often employed in archaeological applications of CSA. We agree with Guiry (2012: 359) that some issues regarding CSA applications may be remedied by including larger dog sample sizes, though we acknowledge that limited sample availability is often unavoidable given the nature of archaeological remains.

Multilevel Modeling Analysis of Isotope Data

This paper demonstrates advantages of the multilevel modeling approach to isotope data. For instance, although our primary interest lies in household-level effects (e.g., wealth) and correlations, the multilevel modeling approach allows us to model outcomes at the primary unit of analysis: individual hair samples. This approach allows us to incorporate appropriate individual-level predictors, such as *age* and *sex*, and the approach also circumvents the statistical problems that sometimes ensue from relying on averages and aggregations (Pollet et al. 2014). We recognize that the limited sample sizes that characterize archaeological studies may necessitate statistical compromises, but we advocate increased use of multilevel modeling for research on stable isotopes.

Possible extensions of our approach include adding complementary isotope data, such as sulfur, oxygen, and strontium isotopes, among others (e.g., Somerville and Froehle 2011). Correlations across these responses could then be calculated at all levels of the data hierarchy, much like we have calculated household-level correlations for people and dogs as well as individual-level correlations. As seen in the supplemental materials, multivariate response models are relatively straightforward to fit using *brms* and comparable software packages.

We have used "random coefficient" models to distinguish household-level effects of people and dogs. This approach could be extended to nearly any categorical distinction between members of a

higher-level grouping. For example, if there were substantive interests in the diets of males and females at a large number of archaeological sites (e.g., Reitsema and Vercellotti 2012, Pearson et al. 2013) our base model could be adapted to examine site-level variation in gender-related differences.

8. Conclusions

Our study shows that dog diets from two neighboring horticulturalist communities in Nicaragua reflect the general diet of humans at the sites, but do not necessarily correlate with the diets of their owners. This suggests that archaeological applications of CSA may work on the site level via averaging of human and dog diets, but may not hold on a household or intra-household level (e.g., Ames et al. 2015). In particular, our results suggest that while CSA may provide some generalized proxy of human diets at a site, it potentially misses more nuanced variation, such as those related to social stratification. For example, at our sites human diets vary positively with wealth in ways that dogs' diets do not, suggesting that CSA may not capture dietary indicators of wealth inequality in the human population. These results indicate that CSA can allow some general conclusions about human dietary practices, but should be used with caution due to a variety of factors primarily associated with the varied treatment of dogs across cultural contexts.

Potential issues with CSA may be largely related to individual-level versus population-wide approaches. Our study included the sampling of a total population of dogs, allowing for the full range of dietary variation. Limited sampling in an archaeological context cannot necessarily control for the possibility of sampling dogs on extreme ranges of this dietary spectrum. How many samples are enough to account for this variability, an ongoing dilemma in archaeology, is unclear. A previous isotope study of populations from these same sites (Tankersley and Koster 2009) suggested humans and dogs in the same household had the same diet, based on a sample size of five humans and one dog. It is now clear that this preliminary result does not hold given an analysis of the broader population, highlighting potential spurious inferences made from small CSA sample sizes. Paradoxically, the only way to confirm whether a valid surrogacy effect is being identified is to analyze the human isotopes as well, largely negating the advantages of CSA methods.

A contribution of this study is that CSA does not apply in all socio-ecological contexts, and archaeologists need to be cautious when considering dogs as proxies. As has been noted previously (e.g., Bocherens et al. 2000, Eriksson and Zagorska 2003, Eriksson 2004, Guiry 2012, Guiry and Grimes 2013), it is questionable whether CSA can work consistently given the varied treatment of dogs in different settings. In some archaeological contexts, dogs were revered and treated as family; in others they were considered pests or butchered and eaten (Morey 2010, Perri 2014, Perri 2017). As an example of these considerations, although CSA works in a broad sense for our Nicaraguan study sites, on a more precise scale the diets of dogs do not closely reflect the diets of their owners.

Ultimately, the use of CSA is dependent on a firm understanding of the cultural context, the resolution of the dietary proxy that one is trying to obtain, and the use of additional lines of evidence (e.g., faunal remains, macrobotanicals, residue analysis). With enough samples, dog diets are evidently likely to reflect the general diet of humans at a site, but it is unclear what the approach can contribute beyond the dietary information provided by zooarchaeological and archaeobotanical analyses. The approach appears most useful in the identification of C_4 plant consumption, such as maize and millet, in the absence of other evidence, but seemingly only at substantial levels of consumption. There is also a need for agreement about the threshold at which dog dietary isotope values are considered close enough to human values to be viable proxies. Many CSA analyses show dog values within 2-3‰ of human values in both $\delta^{15}N$ and $\delta^{13}C$ (Guiry 2012), which raises questions about the usefulness of dogs as proxies because such differences can be substantial enough to reflect separate trophic levels (Bocherens and Drucker 2003, Hedges and Reynard 2007). Additional applications of the CSA model to other

ethnographic studies, particularly across a range of cultures and environments, will continue to clarify the ways in which CSA may or may not be useful in archaeological contexts.

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References Cited

Al-Bagdadi, F. A., C. W. Titkemeyer, and J. E. Lovell. "Hair follicle cycle and shedding in male beagle dogs." *American Journal of Veterinary Research* 38.5 (1977): 611-616.

Allitt, Sharon, R. Michael Stewart, and Timothy Messner. "The utility of dog bone (*Canis familiaris*) in stable isotope studies for investigating the presence of prehistoric maize (*Zea mays* ssp. *mays*): a preliminary study." *North American Archaeologist* 29.3 (2008): 343-367.

Ames, Kenneth M., et al. "Stable isotope and ancient DNA analysis of dog remains from Cathlapotle (45CL1), a contact-era site on the Lower Columbia River." *Journal of Archaeological Science* 57 (2015): 268-282.

Andersen, David B. *The use of dog teams and the use of subsistence-caught fish for feeding sled dogs in the Yukon River drainage, Alaska*. Alaska Department of Fish and Game, Division of Subsistence, 1992.

Barton, Loukas, et al. "Agricultural origins and the isotopic identity of domestication in northern China." *Proceedings of the National Academy of Sciences* 106.14 (2009): 5523-5528.

Belt, Thomas. *The Naturalist in Nicaragua*. London: J.M Dent & Sons (1911).

Bentley, R. Alexander. "Strontium isotopes from the earth to the archaeological skeleton: a review." *Journal of Archaeological Method and Theory* 13.3 (2006): 135-187.

Bergman, Roland W. *Amazon Economics: The Simplicity of Shipibo Indian Wealth*. University Microfilms, 1980.

Bocherens, Hervé, and Dorothée Drucker. "Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems." *International Journal of Osteoarchaeology* 13.1- 2 (2003): 46-53.

Bocherens, Hervé, Marjan Mashkour, and Daniel Billiou. "Palaeoenvironmental and archaeological implications of isotopic analyses (13C, 15N) from Neolithic to Present in Qazvin Plain (Iran)." *Environmental Archaeology* 5.1 (2000): 1-19.

Bol, Roland, and Christian Pflieger. "Stable isotope (13C, 15N and 34S) analysis of the hair of modern humans and their domestic animals." *Rapid Communications in Mass Spectrometry* 16.23 (2002): 2195-2200.

Bürkner, Paul-Christian. "brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical* Software 80(2017): 1-28.

Burleigh, Richard, and Don Brothwell. "Studies on Amerindian dogs, 1: carbon isotopes in relation to maize in the diet of domstic dogs from early Peru and Ecuador." *Journal of Archaeological Science* 5.4 (1978): 355-362.

Byers, David A., et al. "Stable isotope chemistry, population histories and Late Prehistoric subsistence change in the Aleutian Islands." *Journal of Archaeological Science* 38.1 (2011): 183-196.

Cannon, Aubrey, Henry P. Schwarcz, and Martin Knyf. "Marine-based subsistence trends and the stable isotope analysis of dog bones from Namu, British Columbia." *Journal of Archaeological Science* 26.4 (1999): 399-407.

Cheung, Christina, et al. "Examining social and cultural differentiation in early Bronze Age China using stable isotope analysis and mortuary patterning of human remains at Xin'anzhuang, Yinxu." *Archaeological and Anthropological Sciences* 9.5 (2017): 799-816.

Choy, Kyungcheol, and Michael P. Richards. "Stable isotope evidence of human diet at the Nukdo shell midden site, South Korea." *Journal of Archaeological Science* 36.7 (2009): 1312-1318.

Clutton-Brock, Juliet, and Nanna Noe-Nygaard. "New osteological and C-isotope evidence on Mesolithic dogs: companions to hunters and fishers at Star Carr, Seamer Carr and Kongemose." *Journal of Archaeological Science* 17.6 (1990): 643-653.

Cooper, Catherine G., et al. "Economic and demographic predictors of dietary variation and nutritional indicators in Nicaragua." *American Journal of Human Biology* (2018): e23125.

Crocker, William Henry. *The Canela (Eastern Timbira), I: An Ethnographic Introduction*. Vol. 1. Washington, DC: Smithsonian Institution Press, 1990.

Descola, Philippe. *In the Society of Nature: A Native Ecology in Amazonia*. Vol. 93. Cambridge University Press, 1996.

DeNiro, Michael J. "Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction." *Nature* 317.6040 (1985): 806-809.

DeNiro, Michael J., and Samuel Epstein. "Influence of diet on the distribution of carbon isotopes in animals." *Geochimica et cosmochimica acta* 42.5 (1978): 495-506.

DeNiro, Michael J., and Samuel Epstein. "Influence of diet on the distribution of nitrogen isotopes in animals." *Geochimica et cosmochimica acta* 45.3 (1981): 341-351.

Diaz, Sandra F., et al. "An analysis of canine hair regrowth after clipping for a surgical procedure." *Veterinary Dermatology* 15.1 (2004): 25-30.

Dong, Yu, et al. "Shifting diets and the rise of male-biased inequality on the Central Plains of China during Eastern Zhou." *Proceedings of the National Academy of Sciences* (2017): 201611742.

Dumont, J. and M. Hurlich. "Protein, protein, what is done in thy name?" *Working Papers on South American Indians* 3 (1981):19-23.

Edwards, Kim, Dale Allen Walde, and M. Anne Katzenberg. "Searching for Evidence of Maize Consumption at Cluny: Stable Carbon and Nitrogen Isotope Analysis of Dog and Bison Bone Collagen." *Canadian Journal of Archaeology* 40.2 (2016).

Edwards, Richard W., Robert J. Jeske, and Joan Brenner Coltrain. "Preliminary evidence for the efficacy of the Canine Surrogacy Approach in the Great Lakes." *Journal of Archaeological Science: Reports* 13 (2017): 516-525.

Eriksson, Gunilla. "Part-time farmers or hard-core sealers? Västerbjers studied by means of stable isotope analysis." *Journal of Anthropological Archaeology* 23.2 (2004): 135-162.

Eriksson, Gunilla, and Ilga Zagorska. "Do dogs eat like humans? Marine stable isotope signals in dog teeth from inland Zvejnieki." *Mesolithic on the Move*: *Papers Presented at the Sixth International Conference on the Mesolithic in Europe, Stockholm 2000*, by Lars Larsson, Hans Kindgren, Kjel Knutsson, David Loeffler, Agneta Akerlund, editors (2003).

Fahy, Geraldine E., et al. "Stable nitrogen isotope analysis of dentine serial sections elucidate sex differences in weaning patterns of wild chimpanzees (Pan troglodytes)." *American Journal of Physical Anthropology* 153.4 (2014): 635-642.

Favarato, Evandro S., and Lissandro Gonçalves Conceição. "Hair cycle in dogs with different hair types in a tropical region of Brazil." *Veterinary Dermatology* 19.1 (2008): 15-20.

Fiorello, Christine V., Andrew J. Noss, and Sharon L. Deem. "Demography, hunting ecology, and pathogen exposure of domestic dogs in the Isoso of Bolivia." *Conservation Biology* 20.3 (2006): 762-771.

Fiorello, Christine V., et al. "Multiple-host pathogens in domestic hunting dogs in Nicaragua's Bosawás Biosphere Reserve." *Acta Tropica* 167 (2017): 183-190.

Forline, Louis Carlos. *The Persistence and Cultural Transformation of the Guajá Indians: Foragers of Maranhao State, Brazil*. Ph.D. Dissertation, University of Florida (1997).

Gelman, A., Stern, H. S., Carlin, J. B., Dunson, D. B., Vehtari, A., & Rubin, D. B. *Bayesian Data Analysis*. Chapman and Hall/CRC. (2013).

Gini, Corrado. "Variabilità e mutabilità." *Reprinted in Memorie di metodologica statistica (Ed. Pizetti E, Salvemini, T). Rome: Libreria Eredi Virgilio Veschi* (1912).

Gosden, Chris, and Christina Pavlides. "Are islands insular? Landscape vs. seascape in the case of the Arawe Islands, Papua New Guinea." *Archaeology in Oceania* (1994): 162-171.

Guiry, Eric J. "Dogs as analogs in stable isotope-based human paleodietary reconstructions: a review and considerations for future use." *Journal of Archaeological Method and Theory* 19.3 (2012): 351-376.

Guiry, Eric J. "A canine surrogacy approach to human paleodietary bone chemistry: past development and future directions." *Archaeological and Anthropological Sciences* 5.3 (2013): 275-286.

Guiry, Eric J., and Vaughan Grimes. "Domestic dog (Canis familiaris) diets among coastal Late Archaic groups of northeastern North America: a case study for the canine surrogacy approach." *Journal of Anthropological Archaeology* 32.4 (2013): 732-745.

Gunaratnam, Parameswaran, and G. T. Wilkinson. "A study of normal hair growth in the dog." *Journal of Small Animal Practice* 24.7 (1983): 445-453.

Hedges, Robert EM, and Linda M. Reynard. "Nitrogen isotopes and the trophic level of humans in archaeology." *Journal of Archaeological Science* 34.8 (2007): 1240-1251.

Hedges, Robert EM, Jonathon Thompson, and Bradley D. Hull. "Stable isotope variation in wool as a means to establish Turkish carpet provenance." *Rapid Communications in Mass Spectrometry* 19.22 (2005): 3187-3191.

Hedges, Robert, Elaine Rush, and William Aalbersberg. "Correspondence between human diet, body composition and stable isotopic composition of hair and breath in Fijian villagers." *Isotopes in Environmental and Health Studies* 45.1 (2009): 1-17.

Hidalgo-Mihart, Mircea G., et al. "Historical and present distribution of coyote (Canis latrans) in Mexico and Central America." *Journal of Biogeography* 31.12 (2004): 2025-2038.

Hogue, S. Homes. "Corn dogs and hush puppies: diet and domestication at two protohistoric farmsteads in Oktibbeha County, Mississippi." *Southeastern Archaeology* (2003): 185-195.

Hogue, S. H. "Carbon isotope and microwear analysis of dog burials: Evidence for maize agriculture at a small Mississippian/Protohistoric site." *Integrating Zooarchaeology: Proceedings of the 9th ICAZ conference, Durham*. 2002.

Holt, Flora L., Richard E. Bilsborrow, and Ana Isabel Oña. "Demography, household economics, and land and resource use of five indigenous populations in the Northern Ecuadorian Amazon: a summary of ethnographic research." *Occasional Paper, Carolina Population Center. Chapel Hill, NC: University of North Carolina* 87 (2004).

Howard, Catherine. *Wrought Identities: The Waiwai Expeditions in Search of the "Unseen Peoples" of Northern Amazonia*. Ph.D. Dissertation, University of Illinois, Chicago (2001)

Hublin, Jean-Jacques, et al. "Suggested guidelines for invasive sampling of hominid remains." *Journal of Human Evolution* 55.4 (2008): 756-757.

Jahren, A. Hope, et al. "An isotopic method for quantifying sweeteners derived from corn and sugar cane." *The American Journal of Clinical Nutrition* 84.6 (2006): 1380-1384.

Jay, Mandy, and Michael P. Richards. "Diet in the Iron Age cemetery population at Wetwang Slack, East Yorkshire, UK: carbon and nitrogen stable isotope evidence." *Journal of Archaeological Science* 33.5 (2006): 653-662.

Katzenberg, M. Anne. "Stable isotope analysis of animal bone and the reconstruction of human palaeodiet." *Diet and subsistence: Current archaeological perspectives. Proceedings of the 19th Annual Conference of the Archaeological Association of the University of Calgary*. 1988.

Katzenberg, M. Anne. "Stable isotope analysis of archaeological faunal remains from southern Ontario." *Journal of Archaeological Science* 16.3 (1989): 319-329.

Katzenberg, Mary Anne. "Destructive analyses of human remains in the age of NAGPRA and related legislation." *Out of the Past: The History of Human Osteology at the University of Toronto. Scarborough, CITDPress, University of Toronto at Scarborough* (2001).

Katzenberg, M. Anne. "Prehistoric maize in southern Ontario." *Histories of Maize: Multidisciplinary Approaches to the prehistory, linguistics, biogeography, domestication, and evolution of maize, editado por John E. Staller, Robert H. Tykot y Bruce Benz* (2006): 263-273.

Katzenberg, M. Anne, et al. "Diet reconstruction of prehistoric hunter-gatherers in the Lake Baikal region." *Prehistoric Hunter-Gatherers of the Baikal Region, Siberia. Philadelphia: University of Pennsylvania Press. p* (2010): 175-91.

Kohn, Eduardo. "How dogs dream: Amazonian natures and the politics of transspecies engagement." *American Ethnologist* 34.1 (2007): 3-24.

Kohn, Matthew J. "Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate." *Proceedings of the National Academy of Sciences* 107.46 (2010): 19691-19695.

Koshear, J. *Guaymi Agriculture, Forest Utilization and Ethnobotany in Coto Brus, Costa Rica: An Analysis of Sustainability*. Ph.D. Dissertation, University of California (1995).

Koster, Jeremy M. "Assessing the sustainability of Baird's Tapir hunting in the Bosawas Reserve, Nicaragua." *Tapir Conservation* 20 (2006): 23-28.

Koster, Jeremy M. *Hunting and Subsistence Among the Mayangna and Miskito of Nicaragua's Bosawas Biosphere Reserve*. PhD dissertation. Penn State University (2007)

Koster, Jeremy M. "Hunting with dogs in Nicaragua: an optimal foraging approach." *Current Anthropology* 49.5 (2008a): 935-944.

Koster, Jeremy. "The impact of hunting with dogs on wildlife harvests in the Bosawas Reserve, Nicaragua." *Environmental Conservation* 35.3 (2008b): 211-220.

Koster, Jeremy. "Hunting dogs in the lowland Neotropics." *Journal of Anthropological Research* 65.4 (2009): 575-610.

Koster, Jeremy. "Interhousehold meat sharing among Mayangna and Miskito horticulturalists in Nicaragua." *Human Nature* 22.4 (2011): 394-415.

Koster, Jeremy M., and Kenneth B. Tankersley. "Heterogeneity of hunting ability and nutritional status among domestic dogs in lowland Nicaragua." *Proceedings of the National Academy of Sciences* 109.8 (2012): E463-E470.

Koster, Jeremy M., Mark N. Grote, and Bruce Winterhalder. "Effects on household labor of temporary out-migration by male household heads in Nicaragua and Peru: an analysis of spot-check time allocation data using mixed-effects models." *Human Ecology* 41.2 (2013): 221-237.

Koster, Jeremy M., and George Leckie. "Food sharing networks in lowland Nicaragua: an application of the social relations model to count data." *Social Networks* 38 (2014): 100-110.

Koster, Jeremy, and Andrew Noss. "Hunting dogs and the extraction of wildlife as a resource." *Free-Ranging Dogs and Wildlife Conservation* (2014): 265-285.

Koster, Jeremy, Orlando Bruno, and Jessica L. Burns. "Wisdom of the elders? Ethnobiological knowledge across the lifespan." *Current Anthropology* 57.1 (2016): 113-121.

Kusaka, Soichiro, et al. "Variability in stable isotope ratios in two Late-Final Jomon communities in the Tokai coastal region and its relationship with sex and ritual tooth ablation." *Anthropological Science* 116.2 (2008): 171-181.

Laffoon, Jason E., et al. "A Multi-Isotope Investigation of Human and Dog mobility and diet in the pre-colonial Antilles." *Environmental Archaeology* (2017): 1-17.

Lauer, Matthew Taylor. *Fertility in Amazonia: Indigenous Concepts of the Human Reproductive Process Among the Ye'kwana of Southern Venezuela*. University of California, Santa Barbara, 2005.

LeBeau, Marc A., Madeline A. Montgomery, and Jason D. Brewer. "The role of variations in growth rate and sample collection on interpreting results of segmental analyses of hair." *Forensic Science International* 210.1 (2011): 110-116.

Lee-Thorp, Julia A. "On isotopes and old bones." *Archaeometry* 50.6 (2008): 925-950.

Lupo, Karen D. "A dog is for hunting." *EthnoZooArchaeology: The Past and Present of Human-Animal Relationships*, by Umberto Albarella and Angela Trentacoste, editors. (2012).

Macpherson, A. H., and T. H. Manning. "Pack dogs in the Canadian Arctic." *Polar Record* 10.68 (1961): 509-512.

Mandelbaum, David. "The Plains Cree: an Ethnographic, Historical, and Comparative Study. 1940." *Regina: Canadian Plains Research Centre, U of Regina* (1979).

Mans, Jimmy. *Amotopoan Trails: A Recent Archaeology of Trio Movements*. No. 41. Sidestone Press (2012).

McManus-Fry, Ellen, et al. "Dog-human dietary relationships in Yup'ik western Alaska: The stable isotope and zooarchaeological evidence from pre-contact Nunalleq." *Journal of Archaeological Science: Reports* (2016).

McElreath, Richard. *Statistical Rethinking: a Bayesian Course with Examples in R and Stan*. CRC Press, Boca Raton (2015).

Metzger, Donald J., and Robert V. Morey. "Los Hiwi (Guahibo)." *Los Aborıgenes de Venezuela* 2 (1983): 125-216.

Minagawa, Masao, and Eitaro Wada. "Stepwise enrichment of 15 N along food chains: further evidence and the relation between δ 15 N and animal age." *Geochimica et cosmochimica acta* 48.5 (1984): 1135-1140.

Misarti, Nicole, et al. "Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens." *The Holocene* 19.8 (2009): 1139-1151.

Montiel Ortega, Salvador, Luis Arias, and Federico Dickinson. "La cacería tradicional en el norte de Yucatán: una práctica comunitaria." *Revista de Geografía Agrícola* 29 (1999): 43-52.

Morey, Darcy. *Dogs: Domestication and the Development of a Social Bond*. Cambridge University Press, 2010.

Murray, Matthew L., and Margaret J. Schoeninger. "Diet, status, and complex social structure in Iron Age Central Europe: Some contributions of bone chemistry." *Tribe and Polity in Late Prehistoric Europe*. Springer US, 1988. 155-176.

Noe-Nygaard, Nanna. "δ13C-values of dog bones reveal the nature of changes in man's food resources at the mesolithic-neolithic transition, Denmark." *Chemical Geology: Isotope Geoscience section* 73.1 (1988): 87-96.

O'Connell, Tamsin C., and Robert EM Hedges. "Investigations into the effect of diet on modern human hair isotopic values." *American Journal of Physical Anthropology* 108.4 (1999): 409-425.

O'Connell, Tamsin C., et al. "Isotopic comparison of hair, nail and bone: modern analyses." *Journal of Archaeological Science* 28.11 (2001): 1247-1255.

O'Leary, Marion H. "Carbon isotopes in photosynthesis." *Bioscience* 38.5 (1988): 328-336.

Oberg, Kalervo. "The Terena and the Caduveo of Southern Mato Grosso, Brazil." (1949).

Oelze, Vicky M., et al. "Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis." *Journal of Human Evolution* 66 (2014): 95-106.

Otárola-Castillo, Erik, and Melissa G. Torquato. "Bayesian statistics in archaeology." Annual Review of Anthropology 47 (2018): 435-453.

Pacheco-Cobos, Luis, and Bruce Winterhalder. "Economic benefits of hunting dogs in the context of tropical horticulture." *The 80th Annual Meeting of the Society for American Archaeology*. 2015.

Pearson, Jessica, et al. "Food and social complexity at Çayönü Tepesi, southeastern Anatolia: Stable isotope evidence of differentiation in diet according to burial practice and sex in the early Neolithic." *Journal of Anthropological Archaeology* 32.2 (2013): 180-189.

Pearson, Jessica A., et al. "Stable carbon and nitrogen isotope analysis at Neolithic Çatalhöyük: evidence for human and animal diet and their relationship to households." *Journal of Archaeological Science* 57 (2015): 69-79.

Perri, Angela R. "Global hunting adaptations to early Holocene temperate forests: Intentional dog burials as evidence of hunting strategies." Ph.D. Dissertation. Department of Archaeology, Durham University (2014).

Perri, Angela R. "A typology of dog deposition in archaeological contexts." *Economic Zooarchaeology: Studies in Hunting, Herding and Early Agriculture*. (2017) Oxbow Books.

Petzke, Klaus J., et al. "Carbon and nitrogen stable isotopic composition of hair protein and amino acids can be used as biomarkers for animal-derived dietary protein intake in humans." *The Journal of Nutrition* 135.6 (2005): 1515-1520.

Pollet, Thomas V., et al. "What can cross-cultural correlations teach us about human nature?" *Human Nature* 25.3 (2014): 410-429.

Reitsema, Laurie J., and Giuseppe Vercellotti. "Stable isotope evidence for sex-and status-based variations in diet and life history at medieval Trino Vercellese, Italy." *American Journal of Physical Anthropology* 148.4 (2012): 589-600.

Richards, Michael P., et al. "Isotope analysis of human and animal diets from the Hanamiai archaeological site (French Polynesia)." *Archaeology in Oceania* 44.1 (2009): 29-37.

Rick, Torben C., et al. "Stable isotope analysis of dog, fox, and human diets at a Late Holocene Chumash village (CA-SRI-2) on Santa Rosa Island, California." *Journal of Archaeological Science* 38.6 (2011): 1385-1393.

Savelle, James M. "Cultural and natural formation processes of a historic Inuit snow dwelling site, Somerset Island, Arctic Canada." *American Antiquity* 49.3 (1984): 508-524.

Schoeninger, Margaret J., Michael J. DeNiro, and Henrik Tauber. "Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet." *Science* 220.4604 (1983): 1381-1383.

Schoeninger, Margaret J., and Michael J. DeNiro. "Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals." *Geochimica et Cosmochimica Acta* 48.4 (1984): 625-639.

Schoeninger, Margaret J., and Katherine Moore. "Bone stable isotope studies in archaeology." *Journal of World Prehistory* 6.2 (1992): 247-296.

Schomburgk, Moritz Richard. *Travels in British Guiana, 1840-1844*. Vol. 1. "Daily Chronicle" Office, 1922.

Schulting, Rick J., and Michael P. Richards. "Dogs, divers, deer and diet. Stable isotope results from Star Carr and a response to Dark." *Journal of Archaeological Science* 36.2 (2009): 498-503.

Schurr, Mark R. "Isotopic and mortuary variability in a Middle Mississippian population." *American Antiquity* 57.2 (1992): 300-320.

Schurr, Mark R. "Using stable nitrogen-isotopes to study weaning behavior in past populations." *World Archaeology* 30.2 (1998): 327-342.

Schwartz, Henry P., and Margaret J. Schoeninger. "Stable isotope analyses in human nutritional ecology." *American Journal of Physical Anthropology* 34.S13 (1991): 283-321.

Serpell, James. "From paragon to pariah: Some reflections on human attitudes to dogs." *The Domestic Dog: Its Evolution, Behaviour and Interactions With People* (1995): 245-256.

Smith, Bruce N., and Samuel Epstein. "Two categories of 13C/12C ratios for higher plants." *Plant Physiology* 47.3 (1971): 380-384.

Somerville, Andrew D., Mikael Fauvelle, and Andrew W. Froehle. "Applying new approaches to modeling diet and status: isotopic evidence for commoner resiliency and elite variability in the Classic Maya lowlands." *Journal of Archaeological Science* 40.3 (2013): 1539-1553.

Somerville, Andrew D., and Andrew W. Froehle. "New approaches to investigating ancient Maya diet: a three-isotope model for the reconstruction of dietary protein sources." *American Journal of Physical Anthropology* 144 (2011).

Somerville, Andrew D., et al. "Exploring Patterns and Pathways of Dietary Change: Preferred Foods, Oral Health, and Stable Isotope Analysis of Hair from the Dani of Mulia, Papua, Indonesia." *Current Anthropology* 58, no.1 (2017): 31-56.

Sponsel, Leslie E. "The Hunter and the Hunted in the Amazon: An Integrated Biological and Cultural Approach to the Behavioral Ecology of Human Predation." PhD dissertation. University of Michigan. (1982): 3656-3656.

Stantis, Christina, et al. "Assessing human diet and movement in the Tongan maritime chiefdom using isotopic analyses." *PloS One* 10.3 (2015): e0123156.

Tankersley, Kenneth B., and Jeremy M. Koster. "Sources of stable isotope variation in archaeological dog remains." *North American Archaeologist* 30.4 (2009): 361-375.

Tifental, Emilia. "The Bridge River Dogs: Interpreting aDNA and Stable Isotope Analysis Collected From Dog Remains." MA Thesis. Department of Anthropology, University of Montana (2016).

Tsutaya, Takumi, et al. "Carbon and nitrogen isotope analyses of human and dog diet in the Okhotsk culture: perspectives from the Moyoro site, Japan." *Anthropological Science* 122.2 (2014): 89-99.

Tsutaya, Takumi, and Minoru Yoneda. "Reconstruction of breastfeeding and weaning practices using stable isotope and trace element analyses: a review." *American Journal of Physical Anthropology* 156.S59 (2015): 2-21.

Tucker, Bram, et al. "Inequalities beyond the Gini: Subsistence, social structure, gender, and markets in southwestern Madagascar." *Economic Anthropology* 2.2 (2015): 326-342.

Valkovic, Vlado. *Trace Elements in Human Hair*. Garland STPM Press, 1977.

Van der Merwe, Nikolaas, et al. "Diet and animal husbandry of the Preclassic Maya at Cuello, Belize: isotopic and zooarchaeological evidence." *Biogeochemical Approaches to Paleodietary Analysis* (2000): 23-38.

Van Klinken, Gert J. "Bone collagen quality indicators for palaeodietary and radiocarbon measurements." *Journal of Archaeological Science* 26.6 (1999): 687-695.

Wagley, C. "Welcome of Tears: The Tapirapé Indians of Brazil." *Welcome of Tears: The Tapirapé Indians of Brazil* (1977).

Waterman, A. J., R. H. Tykot, and A. M. Silva. "Stable Isotope Analysis of Diet-based Social Differentiation at Late Prehistoric Collective Burials in South-Western Portugal." *Archaeometry* 58.1 (2016): 131-151.

Werner, Dennis. *Amazon Journey: An Anthropologist's Year Among Brazil's Mekranoti Indians*. Simon & Schuster, 1984.

West, Catherine F., and Christine A. France. "Human and Canid Dietary Relationships: Comparative Stable Isotope Analysis from the Kodiak Archipelago, Alaska." *Journal of Ethnobiology* 35.3 (2015): 519-535.

White, Christine D., et al. "Isotopic evidence for Maya patterns of deer and dog use at Preclassic Colha." *Journal of Archaeological Science* 28.1 (2001): 89-107.

White, Christine D. "Stable isotopes and the human-animal interface in Maya biosocial and environmental systems." *Archaeofauna* 13 (2004).

White, C. D., Longstaffe, F. J., & Schwarcz, H. P. "Social directions in the isotopic anthropology of maize in the Maya region." *Histories of Maize: Multidisciplinary Approaches to the Prehistory, Linguistics, Biogeography, Domestication, and Evolution of Maize* (2006): 143.

Williams, Lana J., Christine D. White, and Fred J. Longstaffe. "Improving stable isotopic interpretations made from human hair through reduction of growth cycle error." *American Journal of Physical Anthropology* 145.1 (2011): 125-136.

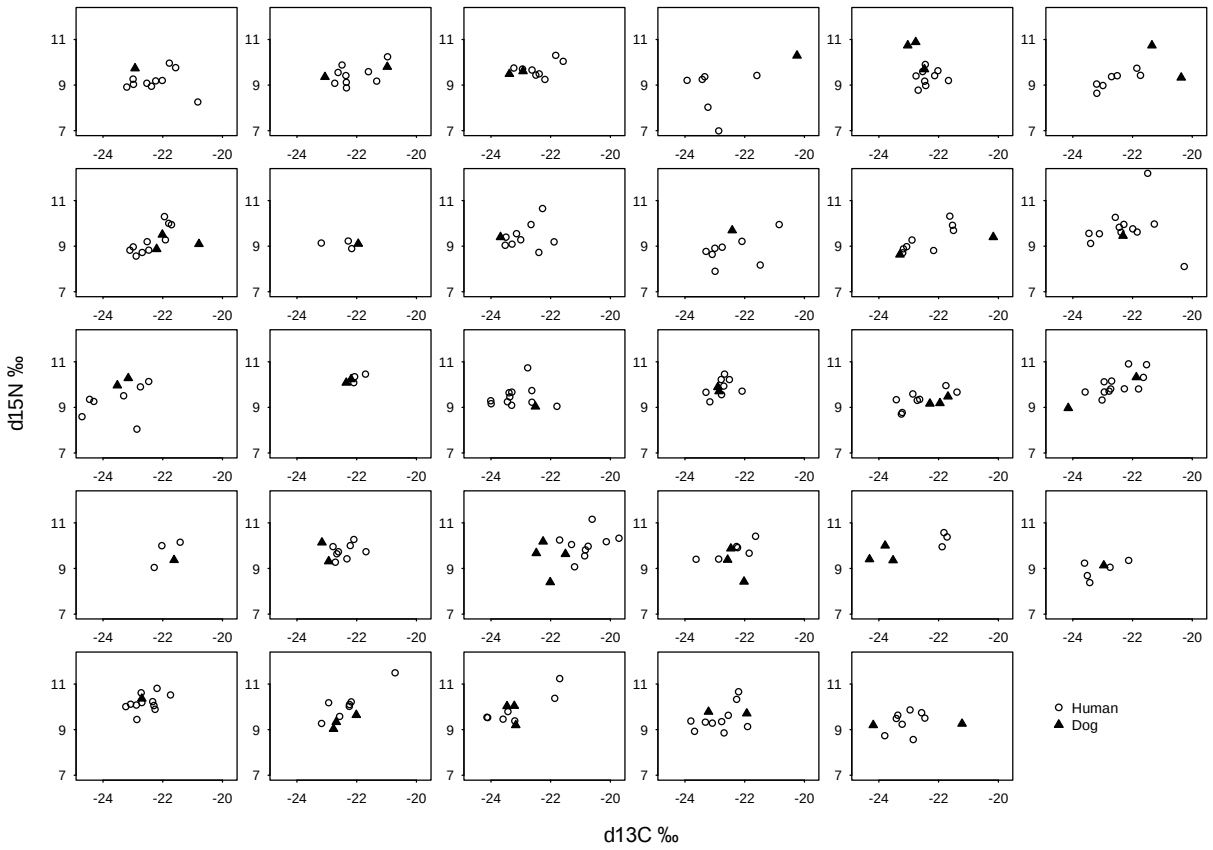
Winking, Jeffrey, and Jeremy Koster. "The Fitness Effects of Men's Family Investments." *Human Nature* 26.3 (2015): 292-312.

Wylie, Alison. *Thinking from Things: Essays in the Philosophy of Archaeology*. Univ of California Press, 2002.

Yoshinaga, Jun, et al. "Stable carbon and nitrogen isotopic composition of diet and hair of Gidra-speaking Papuans." *American Journal of Physical Anthropology* 100.1 (1996): 23-34.

Zagoskin, Lavrentiy A. "Lieutenant Zagoskin's Travels in Russian America, 1842-1844. Arctic Institute of North America. *Anthropology of the North: Translations from Russian Sources*, No. 7, edited by Henry N. Michael." (1967).

Supplemental Figure 1. A Mayangna hunter cuts the footpad from a paca to give to the dog as a food reward for locating the animal.



Supplemental Figure 2. Bi-plots for the 29 households that have at least one dog.

Supplemental Table 1. Raw data for the sampled individuals (humans and dogs; id.code), their associated households (house_code), C/N isotopic values, age, sex, and wealth (log_wealth).